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Managing for biodiversity: impact and action thresholds for invasive plants in natural ecosystems

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Abstract

Some studies examining the impacts of invasive plant species in native plant communities have demonstrated non-linear damage functions, whereby community components, such as species richness, are seemingly unaffected by the presence of an invader until it has attained relatively high levels of abundance, whereupon there is a marked decrease with further increases in abundance. Given chronic limitations in the resources available for managing invasive species, it has been argued that the most damaging invaders would be controlled most efficiently by maintaining their abundances below such threshold levels. Because many impact studies do not involve sampling over a wide range of invader abundances it is not possible to estimate the prevalence of threshold relationships. Furthermore, studies that have employed appropriate sampling methods have shown that different life forms exhibit different threshold responses, indicating that maintenance management for biodiversity values should be designed to protect the most sensitive species or groups of species. Since control costs increase with invader abundance, economic and ecological considerations are aligned when invaders are sustainably maintained at relatively low abundances. Adopting such an approach should also minimise negative impacts where damage functions are linear.

Keywords

Biodiversity asset, diversity, extirpation, maintenance control, species richness, weed impact

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Introduction

It is well-known that invasive alien plants can significantly threaten the structure, function and productivity of natural ecosystems, and are generally associated with declines in diversity and fitness of resident biota (Ehrenfeld 2010, Vilà et al. 2011, Pyšek et al. 2012). However, there is growing evidence that such impacts are highly variable amongst landscape contexts and are modulated by the condition of the recipient native ecosystem (e.g. Mason and French 2007, Pyšek et al. 2012). Although there is little doubt that widespread and dominant invasive plants can adversely affect natural ecosystem properties when at high abundances, evidence that an invasive plant's presence alone causes deleterious changes in the recipient ecosystem's condition is less clear (Barney et al. 2013, Hulme et al. 2013). A key issue is that invasive plant impacts are highly scale-dependent (Powell et al. 2013, Rejmánek and Stohlgren 2015). Indeed, at landscape and continental scales there tends to be a positive rather than negative association between the regional diversity of non-native and indigenous flora (Sax 2002, Maskell et al. 2006, Nobis et al. 2016), which suggests that most introduced plants enrich rather than deplete the diversity of recipient vegetation. Such positive associations at large scales may reflect coincident functional responses of alien and native plants to favourable abiotic (e.g. climate and nutrients) and biotic (e.g. herbivore pressure, pollinator activity) conditions (Sax 2002). Where smaller scales (i.e. those over which management interventions are feasible) are concerned, an important question that must be addressed when assessing invasive plants is: how abundant (in terms of biomass and spatial extent) must a species become before the recipient ecosystem begins to change in response to its invasion? In almost all instances, the rate at which natural ecosystems change (e.g. decline in number of native species) in response to invasion is not known (Barney et al. 2013). Does an ecosystem change at all points along the invasion pathway (i.e. a linear response to invasion), or is there a certain minimum, critical "tipping point" or threshold beyond which an ecosystem changes as the invasive plant becomes dominant?

Given the increasingly high cost and economic burden of controlling invasive species in agricultural and natural ecosystems (e.g. at least $13.6 billion per year in Australia; Hoffmann and Broadhurst 2016), there is a clear need to determine the spatial and temporal scale over which impacts occur, the identities of the invasive plants that drive the greatest impacts, and the ecosystems most vulnerable to change, so that the limited resources for control can be prioritised to areas most likely to be impacted. The very scarce resources available for invasive plant control in natural ecosystems means that the likelihood of eradicating widespread and well-established invaders is diminishingly small (Panetta and James 1999). Prioritisation must be given in such circumstances to controlling widespread alien plants in sites of high conservation priority and containing their spread elsewhere (Cousens 1987). Critical questions that still elude land managers and invasive plant ecologists include: (1) How much of an invasive plant (in terms of cover and biomass) can be retained within an ecosystem without compromising key functions and biodiversity values and (2) When should control be

implemented? The answer to the second question does not follow directly from the answer to the first, as we will show below.

For widespread and dominant invasive plants with demonstrably negative effects on native ecosystems, there is growing evidence that ecosystem responses are non-linear, such that they occur only once a particular level of invasive plant abundance has been exceeded; that is, a negative impact threshold relationship (Alvarez and Cushman 2002, Gooden et al. 2009, Thiele et al. 2010b, McAlpine et al. 2015, Fried and Panetta 2016). In this paper we describe a mechanistic framework for such relationships and explore the role of thresholds in triggering invasive plant control. Our framework explicitly considers alien plants that are widespread across their potential invasive ranges, locally abundant and capable of generating negative impacts in native plant communities.

Ecological framework for invasive species impact thresholds

The concept of invasive species impact thresholds has received attention for at least two decades (see reviews by Adair and Groves 1998, Panetta and James 1999), yet little headway has been made in testing threshold models empirically in the field, or exploring their application to decisions related to invasive plant control. Henry (1994) first suggested that, given limited management resources, invasive populations could be locally contained below an abundance threshold level to prevent the decline in native vegetation or other ecosystem properties. This model assumes that invasive plants interact only weakly with native vegetation at low abundance levels, and invasion deleteriously affects recipient ecosystem properties only once an abundance threshold is breached. Adair and Groves (1998) posited that this threshold could be used to set the maximum tolerable level of infestations and consequently a target for weed control programs.

The prevalence of impact thresholds throughout invaded ecosystems is poorly known. A recent review of biases and errors in assessments of weed impacts on natural ecosystems by Hulme et al. (2013) highlighted that our ability to determine the prevalence, scale, direction and rate of ecosystem change in response to invasive plants is hampered by the fact that the vast majority of extant impact studies do not quantify ecosystem responses along a gradient of alien plant abundance. Rather, most studies tend to compare heavily invaded sites (e.g. where the abundance of the invasive plant relative to native ones exceeds at least 60 or sometimes 80%, e.g. Mason and French 2008, Gooden and French 2014) to non-invaded sites (Hulme et al. 2013). It is thus possible that impact threshold relationships between invasive plant abundance and natural assets, such as native species richness, are more prevalent than is currently recognised, but our sampling efforts are currently inadequate to detect them.

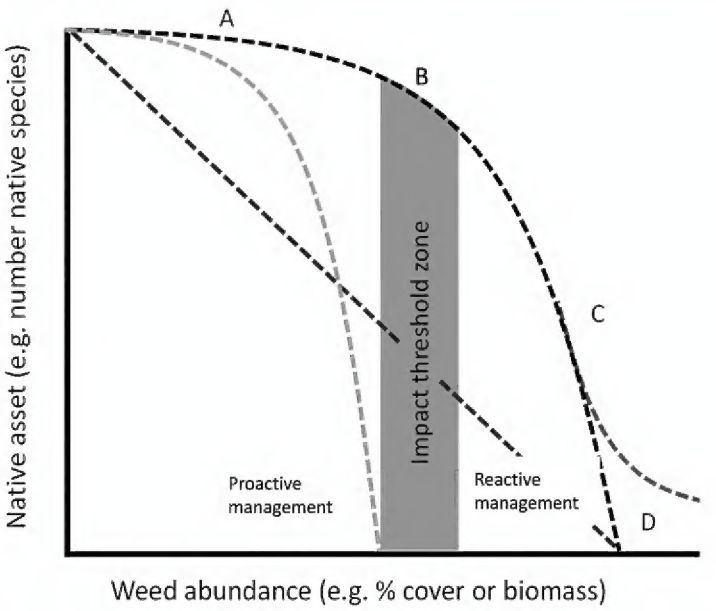
For example, Gooden et al. (2009) sampled vegetation species richness, abundance and composition in wet sclerophyll forest of eastern Australia that was invaded by the thicket-forming shrub *Lantana camara*. Samples were taken across a gradient of *L. camara* cover, to ensure that community change was not biased towards the relatively small proportion of infestations in which *L. camara* cover exceeded 80%. Gooden et al.

(2009) found that there was a striking non-linear decline in the number of native plant species with increasing *L. camara* cover, such that native species loss occurred only once *L. camara* cover exceeded a threshold zone of between 60-80% within the forest. Indeed, some of the highest species richness values occurred when *L. camara* was present in the forest at covers between 20 and 50%, which strongly suggests that this invader is able to coexist with native species at low abundances without exerting significant negative impacts on the community. Importantly, however, threshold effects of *L. camara* varied substantially amongst different native plant functional groups; for example, native vine and herb species richness began to decline significantly at only 70-80% *L. camara* cover, whilst native fern species richness began declining at 30-40% cover. These results indicate that thresholds can vary amongst different life forms within the invaded ecosystem, and furthermore that the maximum tolerable level of an invader should be set at the threshold demonstrated by the most sensitive ecosystem component.

Several other studies have also provided evidence for negative impact thresholds for a variety of invasive plants, including the shrub *Baccharis halimifolia* in Mediterranean saltmarshes (Fried and Panetta 2016), the monocarpic perennial *Heracleum mantegazzianum* in northern European grasslands (Thiele et al. 2010b), the vine *Delairea odorata* in northern Californian coastal scrub and riparian communities (Alvarez and Cushman 2002), and the scrambling herbs *Tradescantia fluminensis, Plectranthus ciliatus* and *Asparagus scandens* in New Zealand temperate forests (McAlpine et al. 2015). Fried and Panetta (2016) found that native species' responses to invasion were complex and, in general, non-linear across a gradient of *B. halimifolia* cover. Species richness declined linearly with increasing *B. halimifolia* cover (indicating a non-threshold relationship), whilst the abundance of native perennial forbs and graminoids declined significantly only when *B. halimifolia* exceeded 80%, i.e. following a threshold relationship. McAlpine et al. (2015) reported that patterns of native plant species decline varied amongst the three weed species in the temperate forest, with only *T. fluminensis* and *P. ciliatus* exerting negative threshold effects on native species richness at approximately 50 % weed volume. It is clear from these studies that rates of species decline and the position of the threshold zone varies from one invasive species to another, and may depend upon the functional identity of the native vegetation within the recipient community. For example, over a broad range of invaded habitats, Hedja (2013) found that annuals, species with taproots, juveniles of tree species and fast-spreading clonal species were impacted least by invasion. Presumably communities with a high proportion of such species would exhibit wider maintenance zones (see Box 1). Other work has shown that species of small stature were most negatively impacted in communities invaded by either *Heracleum mantegazzianum*, *Lupinus polyphyllus* or *Rosa rugosa* (Thiele et al. 2010a).

The ecological processes that underpin impact threshold relationships (Box 1) have as yet not been examined empirically, yet may be framed by two broad questions: (1) What maintains native vegetation diversity or ecosystem function at levels below the weed abundance threshold, and at what point (i.e. threshold) do native species begin to decline (or ecosystem processes change) with increasing weed abundance? Based on

Box 1. Conceptual model for negative impact threshold relationships between invasive plant abundance and a natural asset (e.g. number of native plant species) within the recipient ecosystem.



Invasive species impact threshold relationships can be defined as non-linear declines in one or more natural ecosystem properties, such as number of native plant species, with increasing weed abundance. The model curve consists of several components:

A. Threshold relationships exist when the quality of a particular natural asset does not significantly change (either positively or negatively) at low levels of invader abundance. At point **A** on the non-linear curve, native plant species are able to coexist with the invasive plant . This initial "zone of maintenance" may vary in extent depending on the type of invaded community, capacity of the native species to withstand invasion and functional activity of the invasive plant. For example, as indicated by the relatively steep light-grey-dotted curve at point **A**, invasive plants that actively engineer one or more ecosystem properties, such as nitrogen-fixing shrubs, may drive native species decline even at low levels of invasion, due to small changes that accumulate through time. In some instances multiple thresholds have been observed (see Fried and Panetta 2016) but we do not consider this phenomenon further.

B. This point lies within the threshold zone: the levels of invasion at which the natural asset in question begins to decrease as weed abundance increases. This represents a transition zone from one natural ecological state (i.e. ecosystem dominated by native species) to an alternative, degraded state (i.e. one dominated by an invasive species, with altered ecosystem properties; Downey and Richardson 2016). As yet, there has been no explicit test of how extensive threshold zones can be or the processes that underpin the transition between the alternative states on either side of the threshold zone.

C. The rate of change (represented by the negative gradient over the stretch of curve at point **C**) once the threshold zone has been exceeded is unknown in most cases, but can be very high. For example, Gooden et al. (2009) found that about two native plants were displaced with every percentage increase in *L. camara* cover above 75%, whilst no detectable change in native species richness occurred up to this cover abundance threshold.

D. The trajectory of the tail-end of a threshold relationship, where weed abundance approaches 100%, has never been examined and therefore is unclear for most invasive species. It is nonetheless an important component of the curve, because it defines the subset of ecological attributes that are tolerant to invasion at high abundances (see Hejda 2013). In some cases, such as with *L. camara*, the negative gradient appears to approach zero native species richness, where the invader completely replaces the native community (Gooden et al. 2009). In other cases (e.g. *T. fluminensis*; McAlpine et al. 2015), rates of loss of native species follow a sigmoidal relationship, whereby the decline in species richness beyond the threshold zone is initially rapid but slows with increasing weed abundance, eventally approaching an asymptote as weed abundance approaches 100%. A negative sigmoidal-threshold relationship occurs where a tolerant subset of native species is retained even at very high invader abundance.

"Proactive management" is undertaken to prevent weed abundance from reaching threshold zone levels. Delaying control until after the weed has attained high levels of abundance (i.e. "reactive management") may result in irreversible loss of particularly sensitive species (Downey and Richardson 2016).

classical competition theory, species will interact weakly at low densities, especially when resources are high or if resource requirements do not overlap strongly in niche space, thereby enabling coexistence. At low densities, an invasive plant's competitive performance against well-established natives may be relatively weak if those native plants have priority access to limited resources and greater resource-use efficiency (e.g. Kardol et al. 2013, Mason et al. 2013). Ecosystems with high levels of resilience to disturbance (such as those with either persistent and dense seed banks or ones that are replenished often by immigrant propagules from adjacent patches of non-invaded vegetation) may have high impact thresholds. This is because any losses of standing native vegetation in response to invasion may be buffered against by recruitment from the seed bank, thus maintaining community diversity (Gioria and Pyšek 2016). (2) What are the mechanisms underpinning the dynamic transition across the threshold zone from a rich, functional natural ecosystem to one dominated by an invasive plant with reduced natural value? The threshold zone most likely represents a rapid, dynamic shift from one state (i.e. natural ecosystem) to an alternative, degraded one (i.e. invaded ecosystem). Such a rapid (rather than a gradual and linear) shift across the threshold may be driven by high levels of disturbance and, in some cases, positive feedback mechanisms (e.g. at high densities, invasive grasses of semi-arid woodlands can boost wildfire severity and frequency, which accelerates native species loss and facilitates further invasion; Rossiter et al. 2003), or may simply represent the point at which multiple native species disappear simultaneously as invasion increases. The mechanisms by which alien species reduce diversity are likely to vary according to vegetation successional status, with competition for resources more prominent in the mid- to late-successional stages (Catford et al. 2012).

Thresholds and management for biodiversity values

Interest in the application of thresholds to the management of weeds in agricultural systems developed as an extension of their use in managing arthropod pests in crops (Norris 1999). Fundamental differences in the biology of pest animals and weeds, in particular the existence of seed banks in the latter, meant that major differences in population dynamics had to be taken into account if thresholds were to be at all useful. The "economic threshold level" (the point at which economic losses equal the cost of control) proved to be inadequate for crop weed management, essentially because the seeds produced by plants present at sub-threshold densities would contribute to the soil seed bank and hence to the weed burden of future crops. The "economic optimum threshold" proposed by Cousens (1987) was an attempt to include the economic impacts of multiyear population dynamics. Since ultimately a decision needs to be made on when to take action against a pest, the manager will need to determine an "action threshold" (Cousens 1987, Coble and Mortensen 1992). In practice this may combine an economic threshold, a "safety threshold" (allowing a safety margin owing to uncertainty about both economics and weed-related crop losses), and a "visual threshold"

(what is visually acceptable to the land manager) (Norris 1999). Given that natural ecosystems are considerably more complex than their agricultural counterparts, it could be anticipated that the determination of action thresholds in this context would be particularly challenging. That said, where the protection of biodiversity values is the objective, the problem can be framed more simply because its economic dimension can be reduced to the cost of control, particularly where damage is not sufficient to require restoration effort.

Panetta and James (1999) concluded that, regardless of the invasion context, four aspects must be considered in relation to the use of thresholds in weed management, namely: (1) the benefits provided for the system being managed; (2) damage relationships resulting from the presence of weeds; (3) weed population dynamics; and (4) the framing of risk. In general, very little information is available upon which to base predictions of the population dynamics of weeds of natural ecosystems. Furthermore, recruitment of weeds can be highly episodic, with the attendant risk that occasional rapid increases in density could make effective control much more difficult. Hiebert (1997) argued that the urgency of weed control is an important factor in prioritising weed control efforts—urgency being defined in terms of how much of an increase in effort would be required to achieve successful control should action be delayed. We will return to this point below.

Management strategy options—eradication, extirpation and maintenance control

Eradication has been defined as the elimination of every single individual (including propagules) of a species from a defined area in which recolonisation is highly unlikely (Myers et al. 1998). Where the targeted invader is widespread, extirpation (the elimination of all individuals from an area in which the possibility of recolonisation cannot be ignored in practice; Wilson et al. 2017) would be the appropriate strategy. There may be circumstances under which extirpation is both desirable and achievable, for example when a high quality asset is isolated spatially and potential pathways of recolonisation are either inactive or can be managed effectively. In most cases, however, "maintenance management" (controlling an invader to densities at which it can be tolerated; Simberloff 2003) will be the most appropriate response. Where damage functions are non-linear, this would involve ensuring that invader densities lie within the maintenance zone (designated by point **A** in Box 1), i.e. below the impact threshold zone.

The concept of maintenance control for invasive plants in natural ecosystems appears to have originated in relation to the management of aquatic weeds, specifically water hyacinth (*Eichhornia crassipes*) in Florida during the early 1970s. Until then management of water hyacinth had been essentially reactive (see Box 1), whereby the weed was allowed to reach problem levels before control was implemented. Among other negative effects, this management strategy resulted in severe detrital loading from controlled plants. Joyce (1985) reported that maintaining water hyacinth below 5%

cover reduced annual herbicide use by more than 250%, reduced organic sedimentation by up to 400%, and also reduced depressions in dissolved oxygen. Following widespread adoption of maintenance control, relatively little management was necessary by the mid-1980s, reducing environmental and economic impacts. Recolonisation by native plants promoted the restoration of fish and wildlife habitat in many areas (Schardt 2005). The difficulty of detecting and controlling this weed at extremely low densities, the likely presence of a persistent seed bank and potential recolonisation via vegetative propagules meant that maintenance control was the most cost effective management option.

Maintenance control in a terrestrial context was addressed by Goodall and Naudé (1998, p. 116), who defined the maintenance control phase as one "...when priority areas require low annual or biennial commitment to prevent reinfestation (less than 5% cover), or can be maintained using management practices like fire and livestock." For a range of weed life forms and control methods they demonstrated that the cost of labour for keeping weeds to such low densities was considerably less than when control was undertaken at higher densities (Fig. 1) and was the most cost-effective management option when extirpation was not feasible. Similar cost-versus-density relationships have been reported for the control of Australian *Acacia* and *Eucalyptus*, as well as *Pinus*, species in South Africa (Marais et al. 2004).

The timing of maintenance control has a significant bearing upon the retention of biodiversity values. Where a maintenance control regime is commenced following control efforts targeting an invader that has achieved a high level of cover, legacy effects (Corbin and D'Antonio 2012) may occur, depending upon the length of time that the invader has been present. If the targeted species has been dominant for a long time, there is a risk that highly sensitive native species may have become extirpated (Downey and Richardson 2016). Biodiversity values will therefore be best protected if maintenance control is proactive, controlling the invasive plant at its earliest stages of invasion, rather than reactive—implemented to protect a potentially degraded asset.

The aim of maintenance control should be to keep the cover of the targeted species within a range below the impact threshold zone over an indefinite timeframe, without the need for its eradication across the invaded range. The upper limit of this range will be determined largely by two factors, the first being ecological and the second economic. Where the biodiversity value of the asset being managed is very high, there will be a need to protect the life forms (or species) that are most sensitive to the presence of the invader, whether the relevant damage function is linear or non-linear (Fried and Panetta 2016). The second determinant will be the cost of control, which is expected to increase with the cover of the targeted species (Fig. 1). Taking into consideration the fact that managers usually operate under strong budgetary constraints, an argument can be made for approaching the problem from a primarily economic perspective (i.e. managing for a level of invader cover that is least costly to maintain) since economic and biodiversity objectives are essentially concordant. In relation to invasive species population density and economic impact, Yokomizo et al. (2009) have argued that the optimal management effort will minimise the sum of both management and impact

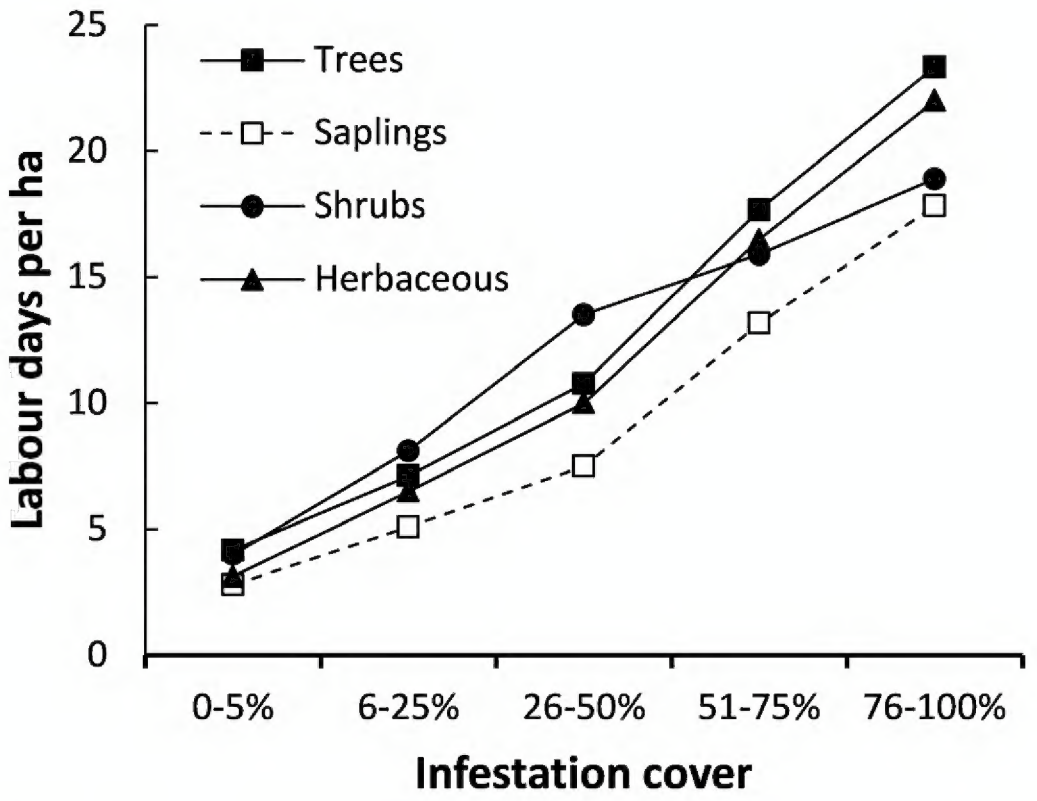


Figure 1. Work rates for control actions in relation to weed cover for different growth habits in KwaZulu Natal, South Africa. Values for each habit are averages for different control methods, calculated from data in Goodall and Naudé (1998). Maintenance control, as defined by the authors, is that undertaken at 0–5% infestation cover.

costs. Note that if the invader is maintained at very low densities, the specific nature of the damage function will become moot.

Tactics for maintenance control differ qualitatively from those employed when extirpation is the management goal. In essence this means that the exacting standards of extirpation, in particular the control of all aboveground plants and the total elimination of seeds and other propagules, can be relaxed (Table 1). While return times (i.e. intervals between consecutive search and control operations) for extirpation must be sufficiently short to prevent reproductive escape (Panetta 2007), some level of seed production would be allowable under maintenance control. For perennial species, fecundity schedules relative to age and size are of relevance, since plants generally produce the smallest number of seeds during their first reproductive event. For example, Osunkoya et al. (2012) found that under the most favourable conditions *Lantana camara* seedlings (10–20 cm) could produce fruits within one growing season. However, for plants growing in the understorey of an open eucalypt forest, fruit production increased markedly with plant size. Small (61–100 cm), medium (101–160 cm) and large (>160 cm) plants produced 34.8 ± 58.1 (mean + sem), 569 ± 27 and 1328 ± 581 fruits respectively.

Species that reproduce vegetatively warrant special consideration, since clonal growth has been shown to influence the magnitude of the impact of non-native plants on native species richness (Vilà et al. 2015). Many invasive aquatic plants proliferate through clonal growth (Barrat-Segretain 1996), but can be readily controlled by some combination of mechanical, chemical and, in some cases, biological control. In a terrestrial context,

Table 1. Tactics for extirpation versus maintenance control. Widespread invaders are generally not good candidates for extirpation because of a continued risk of re-invasion. In the context of asset protection the intensity of control required to keep the invader at maintenance levels will be significantly less than would be the case if the management goal were extirpation.

Activity, process or variable	Extirpation	Maintenance control
Search and control	All growth stages targeted	Largest individuals preferentially targeted
Seed production	Prevented	Reduced
Vegetative reproduction	Reduced or prevented depending on control effectiveness	Reduced
Dispersal	Reduced or prevented as consequence of activities targeting seed production per se	Reduced as consequence of activities targeting largest individuals
Soil seed bank	Eliminated	Controlled as a consequence of reduced seed production
Return time	Determined by generation time of targeted species	Determined by cover and biomass of targeted species

achieving effective control of plants that exhibit clonal growth can be more challenging. Perennial plant species that spread vegetatively can be difficult to manage, especially where potentially more effective control methods (e.g. herbicide application) are not permitted (Schiffleithner and Essl 2016). Even if herbicides are an important component of control tactics, control may be inadequate owing to less than optimal effectiveness of systemic herbicides (Brown and Bettink 2010, Enloe et al. 2013). For such species, care must be taken to prevent the establishment of new plants, an exception to the general guideline that larger plants should be prioritised for control (see Box 2).

Concluding remarks

In this piece we have assumed that the biodiversity values of an asset are known and that a management strategy can be formulated on the basis of this knowledge. When considering the management of widespread serious weeds on a larger scale there is a need for an understanding of the biodiversity values of different assets, as well as the urgency of control (see Hiebert 1997) relative to the degree of threat posed to biodiversity (Downey et al. 2010). The need for further research is manifold. The prevalence of non-linear damage relationships, whether these relate to biodiversity values or ecological functions, will only become apparent by sampling over a broad range of weed abundance in impact studies. The ecological processes that underpin impact threshold relationships are largely unknown and it has yet to be determined whether maintenance control to a level below the threshold really does prevent declines in native species. Finally, there is a need to obtain estimates of maintenance control costs for a range of invasive species life forms and recipient communities so that weed management decisions may be better informed.

Box 2. Guidelines for maintenance control. The standard of control here is less exacting than where extirpation is the management goal, but the underlying principles are similar.

1) **Maintenance control should be undertaken only if there is a commitment to continued management of a valued asset.** As compared to extirpation, where there is a defined management endpoint, maintenance control aims to keep the impact of the invader at an acceptable level. Managers must be prepared to support the latter strategy indefinitely or until an equally effective and more sustainable control method (such as biological control) becomes available.
2) **Control should be implemented in such a way as to minimise the likelihood of rapid increases in weed density.** Disturbance resulting from control measures should be minimised. Larger individuals of the targeted species should be prioritised for control. (See (4) below).
3) **Return times should be geared to the life cycle of the targeted species, with more frequent control operations for species with short pre-reproductive periods.** While the need to prevent reproductive escape is less stringent for maintenance control than for extirpation, control measures should be timed so as to reduce the level of propagule production.
4) **Larger plants should be prioritised for control.** Not only do larger plants contribute more to total cover and thus impact, but they are more fecund than smaller plants, a proportion of which would be pre-reproductive. However, where clonal plants reproduce sexually, care should be taken to detect and control new genets if clones are difficult to manage.
5) **Where travel cost is a significant component of the total cost of management, more time should be spent on site in order to detect and control a larger number of plants.** Budget constraints will make it comparatively more difficult to conduct a maintenance control regime when it is relatively expensive to travel to the asset of concern. By increasing search effort (therefore detecting and controlling smaller plants) it may be possible to achieve an acceptable management outcome with greater return times.

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